

A simple model to study phylogeographies and speciation patterns in space

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In this working paper, we present a simple theoretical framework based on network theory to study how speciation, the process by which new species appear, shapes spatial patterns of diversity. We show that this framework can be expanded to account for different types of networks and interactions, and incorporates different modes of speciation.

Keywords: Phylogeography; Speciation; Networks; Spatial ecology; Macroevolution.

I. MOTIVATION

The peculiar spatial relationship between closely related species was among the first patterns of diversity used to infer evolution. As early as the 1850s, Alfred Wallace noted that the closest relatives were often observed in adjacent yet non-overlapping regions [33, 34]. Wagner and Jordan later relied on a similar observation to argue for the importance of geography and isolation in the formation of new species [3]. And finally, Mayr developed a theory of allopatric speciation, a cornerstone of the modern synthesis, again using similar observations [22, 23]. The relationship between phylogeny and geography has shaped our understanding of the origin of species [3, 19]. It is also crucial to the development of a unified theory of community assembly [26, 29]. Yet, theory remains mostly silent about the subject. Few models can generate phylogeographies, and none can be used to study the effect of complex spatial structures [1]. This is surprising, not only because of the theoretical importance of phylogeography, but also because several phylogenetic methods use geography to infer patterns of speciation [1, 20, 21].

Part of the problem lies in the limitations of traditional mathematical methods: analytical solutions to spatially-explicit models are often only available for the most trivial cases [9]. Thus, we are left with no theoretical framework to study the patterns noted by Wallace, Wagner, and Mayr. In this document, we describe a very simple algorithm to generate phylogeographies in spatial networks. Our approach is inspired by metapopulation theory [13, 14, 17] although the spatio-temporal scale is different: we're interested in the dynamics of populations at the regional scale during long periods. The model will be used to study phylogeographies in various spatial contexts and to develop better tools to understand the relationship between phylogeny and geography.

We use the term “phylogeography” in the general sense: it is the union of phylogenetics with geography.

Our approach emphasizes how spatial patterns of speciation shape biodiversity. It cannot be used to study within-species variations, a major focus of phylogeography [12]. This is more consistent with the field known as comparative phylogeography.

II. MODELING THE LANDSCAPE

We model the landscape as a spatial network of communities. A network is a flexible mathematical object defined as a set of vertices V and a set of edges E , which are used to connect the vertices [27]. Here, the vertices represent communities and the edges denote migration [5–8]. Spatial networks are simply networks in which vertices are embedded in a known topological space [16], in our case a two-dimensional map. Thus, each community is represented by a vertex in the network and to a position on a map. Networks are increasingly common in ecology as they can be used to model complex structures and quantify the effect of clustering, connectivity, and isolation [4, 24, 25, 31]. In particular, isolation is the most important factor in many speciation events [3], making networks well-suited to study patterns of speciation in different contexts [5, 6]. The spatial network can be built in two ways. First, random geometric networks can be generated by randomly placing the vertices on a surface, normally the unit square, and linking all communities within some threshold distance [28]. This technique is used to test network algorithms applied to maps [30]. Second, a real map can be used as a template for a spatial network [4, 24]. This method offers the opportunity to generate predictions specific to a given spatial structure, and test the predictions of our algorithm against empirical data.

III. THE MODEL

A species is divided in populations which are distributed in a network of communities. A species is either present or absent in a community, we do not keep track of the number of individuals. Occupancy thus follows the

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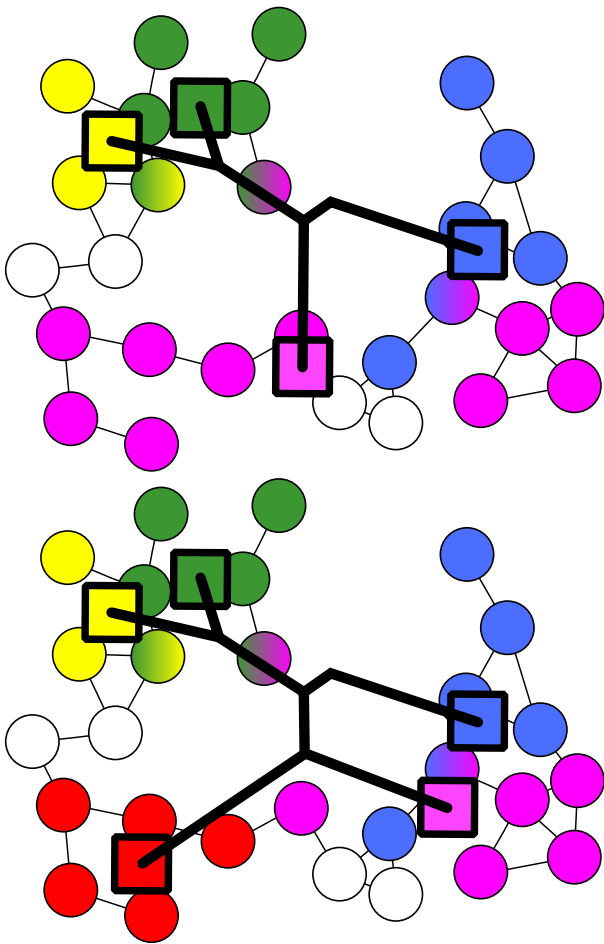


FIG. 1: Top: a phylogeography with four species (yellow, blue, green, pink). The populations are distributed in a spatial network, with each community (circles) hosting populations from 0 or more species. Empty communities are white and a gradient is used for communities with more than one species. The communities are connected by migration (thin black lines). Bottom: a speciation event. The pink species is divided in three groups of populations. Its leftmost group undergoes speciation and a connected subgroup now belongs to a new species (in red).

standard colonization/extinction dynamics of metapopulation theory [13]. For each time step, all populations have the opportunity to colonize adjacent communities (the vertices connected by an edge in the network). The probability of a successful colonization of community x by species i is

$$c(i, x) = c_{max} \exp \left(-\aleph \sum_{j \in \{S_x \setminus i\}} \delta_{ij}^{-1} \right), \quad (1)$$

with $\{S_x \setminus i\}$ being the set of populations present in community x minus i , δ_{ij} is the time since species i and j 's most recent common ancestor, c_{max} is the highest

possible colonization rate and \aleph a positive constant (with $\aleph \geq 0$). \aleph describes the decline of the intensity of interactions with phylogenetic divergence. In short, a higher \aleph makes it difficult for closely related species to coexist. c_{ix} is a very simple function derived from exponential decay. It is based on an old hypothesis by Darwin: closely related species are more likely to compete. It has recently received experimental support [15, 32]. A strong assumption of trait conservatism underlies the model [18]. At each time step, all populations have the same probability e of extinction. Speciation occurs in groups of populations. We define a group as a set of connected populations from the same species (Fig. 1). Each group has a probability v of undergoing speciation. When speciation occurs in a group, a random subset of $[1, n]$ connected populations will speciate, with n being the number of populations in the original group (Fig. 1).

IV. VARIATIONS

The basic model can easily be extended to account for various types of interactions. In this section we briefly discuss a few extensions.

A. Allopatric speciation

Our model is mostly parapatric, with strictly allopatric speciation occurring only with probability $1/n$, with n being the size of the group to speciate. An alternative is to always force allopatric speciation by making the entire group speciate.

B. Sympatric speciation?

With few solid cases of sympatric speciation, and many of them involving important allopatric/parapatric phases [2, 3, 11], it is hard to decide how to do a phenomenological sympatric speciation model. Furthermore, the assumption of strong niche conservatism would be hard to maintain, as niche overlap between diverging populations is one of the hardest challenge for sympatric speciation. Nevertheless, if enough sympatric speciation events can be analyzed, our model could be modified to allow sympatric, parapatric, and allopatric speciation.

C. Variable α

\aleph is fixed in the original model, but it could vary in time and space. For example, smaller regions could have higher \aleph to account for a lower carrying capacity.

D. Variable extinction rates

The extinction rate could have the same form as the colonization rate and be affected by closely related species.

E. Variables v

The speciation rate could decrease with higher diversity (more niches are filled) or increase (“diversity begets diversity”) [10].

F. Growing food webs

The basic idea of using spatial networks and groups of connected populations for speciation could be used to model how complex food webs grow with speciation events. This integration would, however, require many new assumptions and a more sophisticated model for the colonization and extinction rates.

Integrating food web dynamics lead to some difficulties. For example, a trophic model would involve very

different species with potentially different rates of dispersal. The threshold value r used to determine the realized links in the spatial network would have to be different for each group of species. For example, group-specific threshold values could be linked to the niche value (i.e.: smaller species have lower dispersal ranges). A connected random geometric networks could then be generated with the lowest threshold value, ensuring that all networks are fully connected.

G. Positive interactions

Positive interactions between closely related species are also possible, for example in plants. This variation can be achieved by making c_{ix} increase when related species are present.

V. IMPLEMENTATION

An open-source implementation is available on github: <https://github.com/PhDP/wagner>.

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- [1] TG Barraclough and AP Vogler. Detecting the geographical pattern of speciation from species-level phylogenies. *The American Naturalist*, 155(4):419–434, 2000.
 - [2] DI Bolnick and BM Fitzpatrick. Sympatric speciation: models and empirical evidence. *Annual Review of Ecology, Evolution, and Systematics*, 38:459–487, 2007.
 - [3] JA Coyne and HA Orr. *Speciation*. Sinauer Associates, 2004.
 - [4] MRT Dale and M-J Fortin. From graphs to spatial graphs. *Annual Review of Ecology, Evolution, and Systematics*, 41:21–38, 2010.
 - [5] P Desjardins-Proulx and D Gravel. A complex speciation-richness relationship in a simple neutral model. *Ecology and Evolution*, 2(8):1781–1790, 2012.
 - [6] P Desjardins-Proulx and D Gravel. How likely is speciation in neutral ecology? *The American Naturalist*, 179(1):137–144, 2012.
 - [7] EP Economo and TH Keitt. Species diversity in neutral metacommunities: a network approach. *Ecology Letters*, 11:52–62, 2008.
 - [8] EP Economo and TH Keitt. Network isolation and local diversity in neutral metacommunities. *Oikos*, 10:1–9, 2010.
 - [9] BK Epperson, BH McRae, K Scribner, SA Cushman, MS Rosenberg, MJ Fortin, PMA James, M Murphy, S Manel, P Legendre, and MRT Dale. Utility of computer simulations in landscape genetics. *Molecular Ecology*, 19:3549–3564, 2010.
 - [10] DH Erwin. Seeds of diversity. *Science*, 308:1752–1753, 2005.
 - [11] BM Fitzpatrick, JA Fordyce, and S Gavrillets. What, if anything, is sympatric speciation? *Journal of Evolutionary Biology*, 21:1452–1459, 2008.
 - [12] JR Freeland, H Kirk, and SD Petersen. *Molecular Ecology*. Wiley-Blackwell, 2nd edition, 2011.
 - [13] I Hanski. *Metapopulation ecology*. Oxford University Press, 1999.
 - [14] I Hanski. The theories of island biogeography and metapopulation dynamics. In JB Losos and RE Ricklefs, editors, *The Theory of Island Biogeography Revisited*, pages 186–213. Princeton University Press, 2009.
 - [15] L Jiang, J Tan, and Z Pu. An experimental test of darwin’s naturalization hypothesis. *The American Naturalist*, 175:415–423, 2010.
 - [16] K Kobayashi. On the spatial graph. *Kodai Mathematical Journal*, 17(3):511–517, 1994.
 - [17] R Levine. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, 15:237–240, 1969.
 - [18] JB Losos. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters*, 11:995–1003, 2008.
 - [19] JB Losos. *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles*. University of California Press, 2009.
 - [20] JB Losos and RE Glor. Phylogenetic comparative methods and the geography of speciation. *Trends in Ecology and Evolution*, 18(5):220–227, 2003.
 - [21] JD Lynch. The gauge of speciation: on the frequency of modes of speciation. In D Otte and JA Endler, editors, *Speciation and its consequences*, pages 527–553. Sinauer Associates, 1989.
 - [22] E Mayr. *Systematics and the origin of species*. Columbia University Press, New York., 1942.

- [23] E Mayr. *Animal Species and Evolution*. Belknap, Cambridge, MA., 1963.
- [24] ES Minor and DL Urban. Graph theory as a proxy for spatially explicit population models in conservation planning. *Ecological Applications*, 17(6):1771–1782, 2007.
- [25] ES Minor and DL Urban. A graph theory framework for evaluating landscape connectivity and conservation planning. *Conservation Biology*, 22(2):297–307, 2008.
- [26] N Mouquet, V Devictor, C Meynard, L-F Bersier, J Chave, P Couteron, A Dalecky, C Fontaine, D Gravel, O Hardy, F Jabot, S Lavergne, M Leibold, T Muenkemüller, S Pavoine, A Prinzing, A Rodrigues, R Rohr, and E Thebault. Phylogenetic ecology: advances and perspectives. *Biological Reviews*, 2012.
- [27] M Newman. *Networks: An Introduction*. Oxford University Press, 2010.
- [28] M Penrose. *Random Geometric Graphs*. Oxford University Press, 2003.
- [29] SH Rice. A stochastic version of the Price equation reveals the interplay of deterministic and stochastic processes in evolution. *BMC Evolutionary Biology*, 8:262, 2009.
- [30] R Sedgewick. *Algorithms in C++ Part 5: Graph algorithms*. Addison-Wesley Professional, 3rd edition, 2001.
- [31] DL Urban, ES Minor, EA Trembl, and RS Schick. Graph models of habitat mosaics. *Ecology Letters*, 12:260–273, 2009.
- [32] C Violle, DR Nemergut, Z Pu1, and L Jiang. Phylogenetic limiting similarity and competitive exclusion. *Ecology Letters*, 14(8):782–787, 2005.
- [33] AR Wallace. On the monkeys of the amazon. *Proc Zool Soc Lond*, 20:107–110, 1852.
- [34] AR Wallace. On the law which has regulated the introduction of new species. *Ann Magazine Nat Hist Ser 2*, 16:184–196, 1855.